Optimal metabolic patterns in seasonally changing environments

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Abstract

Living organisms are metabolically active throughout their lives; they take up resources from their environment, convert these resources into useful materials and get rid of wastes. The sum of these reactions and processes is called metabolic activity and we can express its speed by the metabolic rate. Species of various kind exhibit great variability in metabolic rate, regarding both its lifetime mean value and its seasonal changes. Metabolic rate is an important factor in population dynamics, because, by multiplicatively influencing the magnitude of the growth rate, it determines how much an individual experiences the favourable or unfavourable environmental conditions. Considering evolutionary competition, the optimal seasonal metabolic pattern is inevitably affected by the amount of resources and the environmental temperature. This raises the question that, under given environmental conditions in a seasonally changing environment, what the evolutionarily stable metabolic pattern is. To examine this question we used the resource-consumer model of MacArthur as a starting point. We extended this model by introducing a seasonal metabolic activity term and a metabolic cost function, which depends on both environmental temperature and metabolic activity. Using an evolutionary algorithm we examined that, starting from a seasonally constant metabolic activity, what evolutionarily stable metabolic pattern emerges via small evolutionary steps, and how the characteristics of the metabolic pattern are affected by the parameters describing the seasonally changing environment (temperature, resources). Among the many evolutionary outcomes at different parameter combinations, we could distinguish three main categories. Two of them supported the traditional view; in favourable and unfavourable environments higher and lower metabolic rate is beneficial, respectively. The third category represents a counterintuitive, more intricate case; under certain environmental conditions metabolic activity exhibits a positive or negative peak when the seasons change. A positive peak occurs, when a sharply increased metabolic activity, in spite of its costs, accelerates the utilisation of the resources found in suddenly increased amounts at favourable seasonal changes. The negative peak can be explained in a similar way, as a phenomenon observable in case of unfavourable seasonal changes.

Hungarian abstract

Az élőlények életfolyamataik során anyagcserét folytatnak; táplálékot vesznek fel környezetükből, szervezetükben átalakítják ezen anyagokat, a felesleges anyagokat pedig leadják. Ezen anyagcsere és reakciófolyamatok összességét metabolikus aktivitásnak nevezzük, melynek sebességét a metabolikus rátával fejezzük ki. Az élővilágban a metabolikus ráta sebessége tekintetében nagy változatosságot tapasztalunk mind az átlagos érték, mind pedig annak évszakos változása szempontjából. Populációdinamikailag a metabolikus ráta értéke azért fontos, mert – a növekedési ráta értékét multiplikatívan befolyásolva – meghatározza, hogy az adott, előnyös vagy előnytelen környezetet egy egyed mennyire intenzíven tapasztalja meg. Az evolúciós versengés szempontjából optimális évszakos metabolikus mintázatot szükségszerűen befolyásolja a források mennyisége, valamint a környezeti hőmérséklet. Ez felveti a kérdést, hogy adott környezeti feltételek mellett, egy évszakosan változó környezetben, mi lehet az evolúciósan stabil metabolikus mintázat. Ezen kérdés vizsgálata céljából a MacArthur féle forrásfelvételi modellt használtuk kiindulópontként, amelyet kiegészítettünk egyrészt az évszakos mebatolikus aktivitást kifejező paraméterekkel, másrészt a metabolikus aktivitás és a környezeti hőmérséklet értékétől függő metabolikus költség függvénnyel. Egy evolúciós algoritmus segítségével azt vizsgáltuk, hogy egyenletes metabolikus aktivitásból kiindulva – kis evolúciós változások során – milyen evolúciósan stabil évszakos metabolikus mintázat alakul ki, és ezen mintázat jellege hogyan függ a környezetet leíró paraméterek (hőmérséklet, forrásmennyiség) évszakos változásától. A különböző paraméterkombinációk esetén létrejövő metabolikus aktivitás mintázatok összehasonlításakor alapvetően három különböző típust tudtunk elkülöníteni. Ezek közül kettő alátámasztja azt a hagyományos nézetet, hogy kedvező környezetben magasabb, míg hátrányos környezetben alacsonyabb metabolikus sebesség az előnyös. A harmadik típus egy alapvetően különböző esetet szemléltet; bizonyos körülmények között a kedvező évszakváltásokkor hirtelen, rövid ideig megemelkedő vagy lecsökkenő metabolikus aktivitás az előnyös. Ennek magyarázata az, hogy az évszakváltozáskor hirtelen megnövekedő forrásmennyiség hatékonyabb felhasználása érdekében előnyös lehet rövid ideig a nagyobb aktivitásból eredő gyorsabb táplálékfelvétel, mely ideiglenesen nagyobb metabolikus költséggel jár. A negatív aktivitás csúcsot ehhez hasonló módon értelmezhetjük, mint kedvezőtlen évszakos változások mellett megfigyelhető jelenséget.

1 Introduction

1.1 Metabolic activity of organisms

Metabolic activity is the process when living organisms take up resources from their environment, convert these into useful materials and get rid of the rest that they can not utilise. For example, most plants need inorganic materials like carbon-dioxide, water, nitrogen, phosphorus, etc., and create their own organic materials. Animals need not just inorganic but organic materials to survive. Plants utilise light energy while animals use the energy of chemical bonds to provide for their energy needs. We can express the speed of these metabolic activities by the metabolic rate, which refers to the overall speed of these life related processes.

Metabolic rate can not be measured directly, but there are some ways to quantify it. Due to the intimate relationship between respiration and metabolic cycles, one handy approach is measuring respiration. Another way is to examine thyroid activity, which also affects almost all metabolic processes. For example the Graves' disease, which frequently involves hyperthyroidism leads to weight loss despite increased appetite, diarrhea, frequent defecation, hyperactivity. A popular expression of metabolic activity is basal metabolic rate (BMR) which is a commonly used term in sport sciences. BMR describes the minimal energy expenditure of endothermic animals at rest, i.e. it is the minimum energy required for the maintenance of endothermic homeostasis.

However, metabolic rate also has a dynamics meaning. An organism having higher metabolic rate experiences its environment more intensively, because with faster metabolism, it takes up and gets rid of more resources in a given time. Therefore, it can grow and reproduce faster, making all its life faster in one word. A lower metabolic rate, on the contrary, leads to slower metabolism, slower resource intake and lower energetic requirements, i.e. slower life.

1.2 Variety in metabolic rate

Metabolic rate can vary greatly between species, but also during the lifetime of an individual. According to the metabolic theory of Gillooly et al. (2001), the whole-organism metabolic rate increases, but mass-specific metabolic rate decreases with body mass. For example, an elephant has greater metabolic rate than a mouse, meaning more food takeup and more dung, but lower metabolic rate for one cell. The size dependent metabolic rate is reflected also in demographic properties: smaller animals have higher mass-specific metabolic rate so higher birth and death rates. That is one reason why laboratories like to use, for instance, mouse as a model animal.

But the size dependence of overall metabolic rate does not express the whole diversity of metabolic patterns in nature. The speed of metabolic activity can change periodically in time in the form of seasonal or daily cycles (Hall, 1832; Geiser & Ruf, 1995; Geiser, 2004). The reason for seasonal metabolic changes can be, that numerous factors of the environment e.g. light, temperature, vapour may change periodically, and creatures are eager to capture the most perfect periods. This can be achieved by increasing or decreasing their metabolic rates at the appropriate times. This metabolic changes can be triggered by some environmental changes or by biological clocks. The mating activity of horseshoe crabs *(Limulus polyphemus)*, for instance, fluctuates with the phase of the moon, the height of the tide, and diurnal changes in daylight (Barlow et al., 1986). It is proposed that they sense spring (mating period) by the daylength or the water temperature. The detection of the daylength may occur by sensing the changing photoperiod and may involve an endogenous circadian oscillator. They sense the relative height of the tides and with high tide they migrate to the shore to mate and build nests. Annual metabolic cycles can be observed during phytoplankton blooming (Evans & Parslow, 1985) or in body composition of migrating birds like cackling geese *(Branta canadensis minima)* (Raveling, 1979). Another interesting annual metabolic cycle is the diapause of insects in a highly seasonal environment (Rinehart et al., 2007). They have to survive in the harsh and rigor environmental conditions of winter without feeding and have to restrict their growth and reproduction to summer. Winter conditions are challenging also for mammals; arctic ground squirrels can hibernate through cold periods by reducing their body temperature to -3°C and their metabolic rate to 1% (Carey et al., 2003). The blooming of plants at springtime is another spectacular manifestation of temporally increased metabolism.

1.3 What is the optimal metabolic rate?

The goal of living organisms is to achieve the maximum level of resource utilisation. Resource utilisation depends on two factors on the level of a populations. One of them is the population density, since the more individuals the population has, the more resources it can take up. The other is the metabolic rate of individuals. If the metabolic rate is higher, the individuals live faster, ingest, but also require, more nutrients. Population density changes are usually slow, compared to environmental changes, but changing the metabolic rate can be fast. But what is the optimal rate of metabolic activity? Favourable/unfavourable environmental conditions are expected to be paired with high/low metabolic rate to maximise benefits or to decrease losses. It means that, if the reproductive rate is positive, i.e. the birth rate is higher than the death rate, metabolic rate should be high. On the other hand, when conditions are harsh, i.e. the birth rate is lower than the death rate, the metabolic rate should be low to minimise losses (Szabó, 2015). In other words, they store the resources of favourable seasons to survive the unfavourable intervals (Chesson, 1994; Amarasekare, 2003).

1.4 Questions

The argument above is valid only when being more or less metabolically active does not imply any costs. It has been shown, that metabolic rates and nearly all other activity rates in biology increase exponentially with temperature (Savage et al., 2004; Brown et al., 2004), due to reaction kinetic effects. This relationship holds only in the range of normal activity, which for almost all organisms lies between 0°C and 40°C (Schmidt-Nielsen, 1997). Any deviance from the passive metabolic rate determined by the ambient temperature causes fitness costs. Therefore, metabolic rate can be costly, depending on both the desired activity level and the ambient temperature. Regarding this metabolic rate associated cost, different strategies can be observed among organisms. On the one hand, the body temperature of ectotherms roughly follows the ambient temperature imposing negligible cost, on the other hand endotherms maintain a nearly constant body temperature imposing additional energetic cost. Note, however, that there exists a continuous strategy range between these two extreme cases. For example, some ectotherms can change their metabolic rate by means of behavioural adaptations, e.g. sunbathing. As an other example, heterotherms are usually in homeotherm state except for shorter hibernation periods. Our aim is to make a step towards explaining this diversity in metabolic patterns. In the present study, using theoretical methods, we examine how the optimal, evolutionarily stable, metabolic pattern may depend on the seasonally changing environmental conditions, including resource abundance and ambient temperature. Our model was a generalised version of the MacArthur competition model (MacArthur, 1969, 1970; May, 1974). Using this model and an evolutionary algorithm we followed the evolution of the metabolic function under different environmental conditions.

2 Methods

2.1 The MacArthur model

The MacArthur model (MacArthur, 1969) describes the dynamics of a set of competing populations by explicitly connecting the dynamics of the consumers and the resource. Considering the case of one resource and N consumers, the model is given by the equations

$$\begin{aligned} \frac{dp_i}{dt} &= c_i p_i \left(u_i R - T_i \right) && \text{(1a)} \\ \frac{dR}{dt} &= gR\left(1 - \frac{R}{K}\right) - \sum_{i=1}^{N} u_i p_i R, && \text{(1b)} \end{aligned}$$

where p_i is the population density of species i, and R is the abundance of the resource. The u parameter stands for the rate at which an individual of species i encounters and eats a given unit of resource, T_i is the threshold resource requirement of species i, and c_i quantifies the conversion from resource to individuals. The model assumes a logistic growth curve for the resource with an intrinsic rate of natural increase g and a resource carrying capacity of K. Assuming that the dynamics of the resource is much faster than that of the populations, the equilibrium resource abundance can be expressed as

$$R^* = K - \sum_i \frac{K}{g} u_i p_i.$$

Following the lines in MacArthur (1969), if we substitute R^* into equation 1 we get the familiar Lotka-Volterra competition model with an explicit expression of the maximal growth rates (k_i) and the competition coefficients (a_{ij}) in terms of resource consumption related parameters

$$\frac{dp_i}{dt} = c_i p_i \left[\underbrace{u_i K - T_i}_{k_i} - \sum_j \underbrace{\frac{K}{g} u_i u_j}_{a_{ij}} p_j \right]. \tag{2}$$

2.2 Metabolic rate dependent model

The speed of metabolic activity, defined as the overall speed of life processes, affects both the resource consumption u_i and resource requirement T_i of individuals. Therefore, we introduced the metabolic rate m_i by expressing these values with the products

$$\begin{aligned} u_i &= m_i u'_i \\ T_i &= m_i T'_i. \end{aligned}$$

where u'_i and T'_i stand for metabolic rate specific values of their non-primed counterparts. Substituting these changes into equation 2 yields

$$\frac{dp_i}{dt} = c_i p_i \left[\underbrace{m_i u'_i K - m_i T'_i}_{k_i} - \sum_j \underbrace{\frac{K}{g} u'_i u'_j m_i m_j}_{a_{ij}} p_j \right]. \tag{3}$$

Notice that, in line with common sense expectations, the metabolic rate of a species acts as a multiplier of the speed of its population dynamical changes. In the followings, without loss of generality, we assume $c_i = 1$ and $u'_i = 1$ for all species. However, maintaining a given metabolic rate can be costly, depending on ambient temperature. Therefore, we need to express resource requirement T'_i as a function of these quantities. We have two guidelines here. First, we assume that maintaining both an extremely high or low metabolic rate can be costly, due to the required morphological, physiological and behavioural adaptations. Second, we assume that the metabolic activity level implying minimal cost increases with temperature. Based on these guidelines, we express the cost of maintaining a particular metabolic activity level as

$$T'_i(m_i, H) = \beta |\alpha H - m_i|, \tag{4}$$

where α and β are two proportionality factors and H stands for environmental temperature. This expression means that the cost of metabolism increases linearly with the deviation from a baseline value, whereas the baseline value itself increases with temperature. The baseline $m_p = \alpha H$ can be interpreted as passive metabolic rate, which does not imply any costs at the given temperature. The proportionality factor α is the metabolic baseline change associated with one degree of temperature change whereas β is the growth rate cost of changing the metabolism with one unit.

We aim to investigate population dynamics in a periodically changing, seasonal environment. In our model, it implies that the resource carrying capacity K, the intrinsic rate of natural increase of the resources g and the temperature H are not scalar values anymore, but become periodic functions, characterising the seasonally changing conditions. Similarly, the metabolic rate of a species is described by its periodic, seasonally changing metabolic function. Let us denote the length of the period of environmental changes by L. For notational convenience let us introduce a new variable, $\tau = \frac{t \bmod L}{L} \in (0, 1)$, which expresses the elapsed time fraction of a period, with zero and one corresponding to the beginning and the end of a period, respectively. Incorporating these considerations into equation 3, our model is given by the equation

$$\frac{dp_i}{dt} = p_i \left[m_i(\tau)K(\tau) - m_i(\tau)T_i'(\tau) - \sum_j \frac{K(\tau)}{g(\tau)} m_i(\tau)m_j(\tau)p_j \right] \tag{5}$$

where the metabolic cost function is

$$T_i'(\tau) = \beta|\alpha H(\tau) - m_i(\tau)|.$$

However, after some mathematical rearrangements it can be easily noted that the change of the resource carrying capacity K and the intrinsic rate of natural increase of the resources g affect the equilibrium state of the population abundance in a similar way. This means that following the law of parsimony we only need one of these functions in our model to achieve our aims. Thus we excluded the resource carrying capacity K and kept the function of the intrinsic rate of natural increase of the resources g which, for simplicity, will be referred to as resource renewal rate from now on. This concludes the explanation of our model which is the following:

$$\frac{dp_i}{dt} = p_i \left[m_i(\tau) - m_i(\tau)\beta|\alpha H(\tau) - m_i(\tau)| - \sum_j \frac{1}{g(\tau)} m_i(\tau)m_j(\tau)p_j \right] \tag{6}$$

2.3 Evolutionary algorithm

We are interested in the evolution of the metabolic function in different environments, characterised with particular seasonal resource renewal rate and temperature changes. To answer this question, we simulated the course of natural selection in different environments with an evolutionary alogrithm consisting of the following steps:

1. Assume an initial resident population with constant metabolic rate throughout the period ($m_1(\tau) = 1$).
2. Calculate the equilibrium state of the resident population by numerical integration of equation 6.
3. Introduce a very small mutant population with metabolic function $m_2(\tau)$. The metabolic function of the mutants is slightly different than the resident one; m_2 is obtained from m_1 by randomly decreasing or increasing its value by a small amount of 0.01 in a random interval of length $L/100$.
4. Calculate the equilibrium state of the resident and the invader population by numerical integration of equation 6. If the mutant population outcompetes the resident one, it becomes the new resident population.
5. Go back to step 2 until evolution of the metabolic function comes to a halt.

These steps are illustrated on the following page in Figure 1. The simulations were written in the Python programming language (version 2.7) (Rossum, 1995).

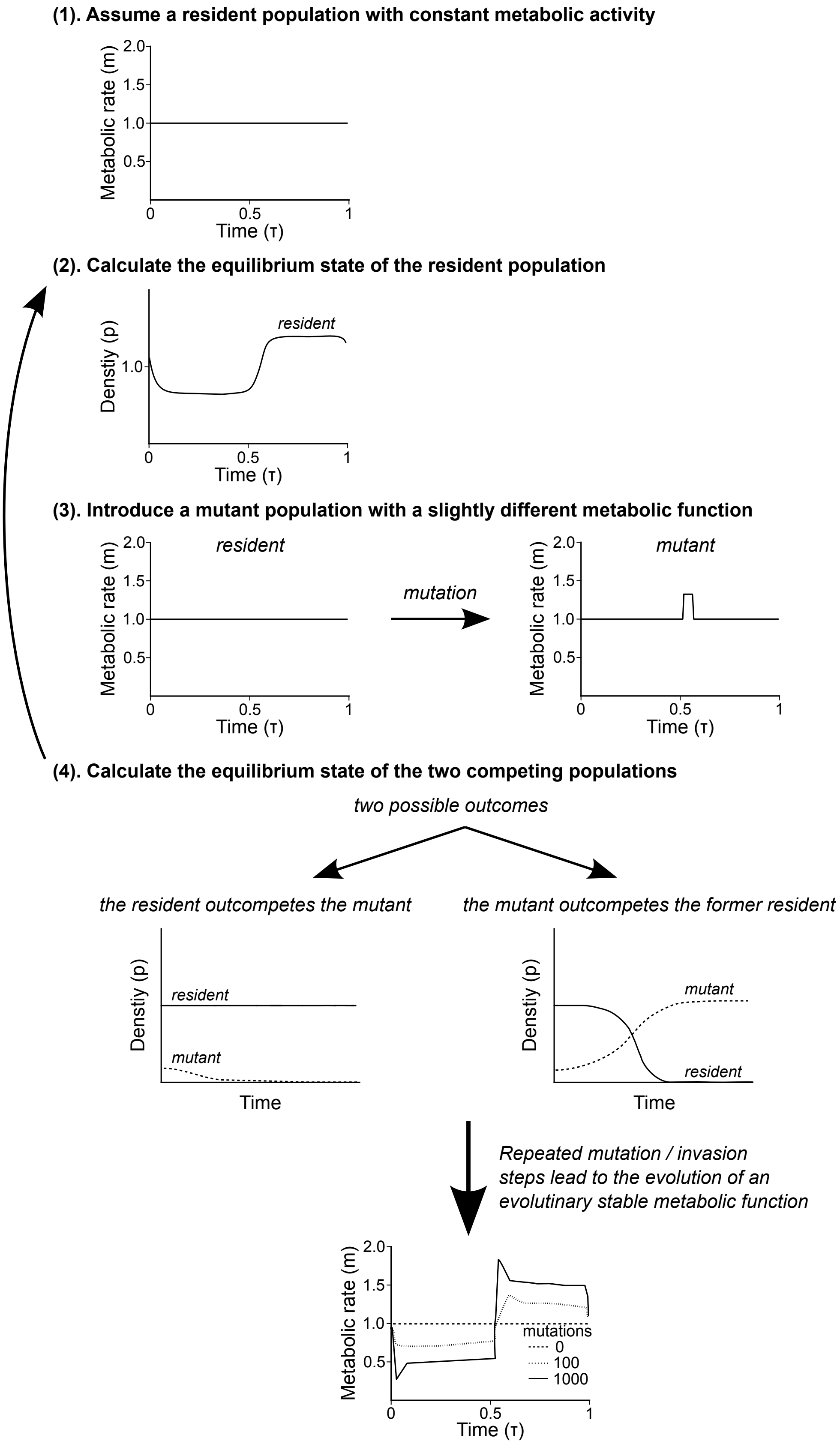


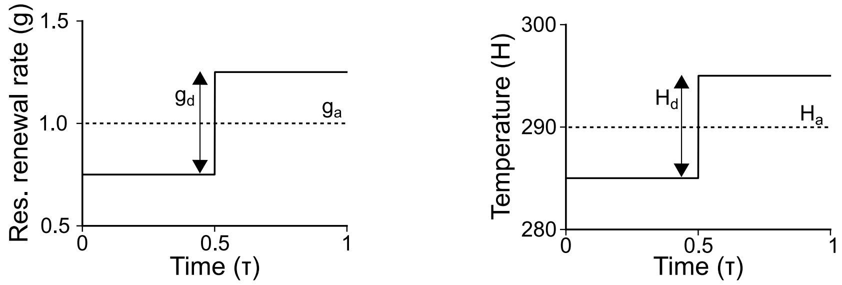
Figure 1: Flowchart of the evolutionary algorithm.

2.4 Parameters

We ran the evolutionary algorithm with different parameter combinations, corresponding to different environments and metabolic constraints (Table 1). In all cases, without loss of generality, we assumed a constant unit value for both the resource conversion efficiency c and the resource uptake rates u_i. For simplicity, we assumed that there are two seasons within a whole period with different conditions, but there are no changes within the seasons. Therefore both the g and H functions were characterised by their yearly average values g_a, H_a and the differences between the seasons g_d, H_d. For each environment, we repeated the calculations with different β metabolic cost values. We had $\alpha = 1/290$ in all cases, because only the product αH has an effect on the dynamics. Considering all the possible combinations of the different values of these six parameters we had 216 different parameter sets altogether.

Table 1: Parameters of the model with the interpretation of the environmental parameters g_a, g_d, H_a and H_d.

Name	Notation	Value(s)
Resource renewal rate	$g(\tau)$	$g_a \pm g_d/2$
– average	g_a	1, 2
– difference	g_d	0, 0.5, 1.0
Ambient temperature	$H(\tau)$	$H_a \pm H_d/2$
– average	H_a	280, 290, 300
– difference	H_d	0, 10, 20
Exchange ratio between temperature and passive metabolic activity	α	1/290
Growth rate cost of one unit of metabolic activity	β	0, 0.01, 0.1, 1.0



3 Results

Performing the evolutionary analysis, we obtained 216 m^* functions being the evolutionarily stable seasonal metabolic patterns for the different parameter combinations. Comparing these outcomes we could distinguish three fundamentally different metabolic function types, which will be discussed in turn.

3.1 Uniform metabolic rate

In several cases, the evolutionarily stable metabolic pattern was a uniform rate throughout the whole period, with zero variation (Figure 2). It evolves in the following two cases:

(a) there is no temperature difference between the two seasons, the cost of metabolic activity is high, and the resource renewal rate difference between the seasons is modest,

(b) there is no resource renewal rate difference between the seasons and the cost of metabolisms is negligible.

In the first case, the uniform metabolism evolves because any deviance from the environmentally determined passive metabolic level would be too costly, and could not be compensated by any possible benefits from increased resource consumption. The second condition expresses that if there is no resource renewal rate difference between the seasons, there is no driving force for increased or decreased metabolism at seasonal shifts, but only if keeping a constant activity level does not imply any costs.

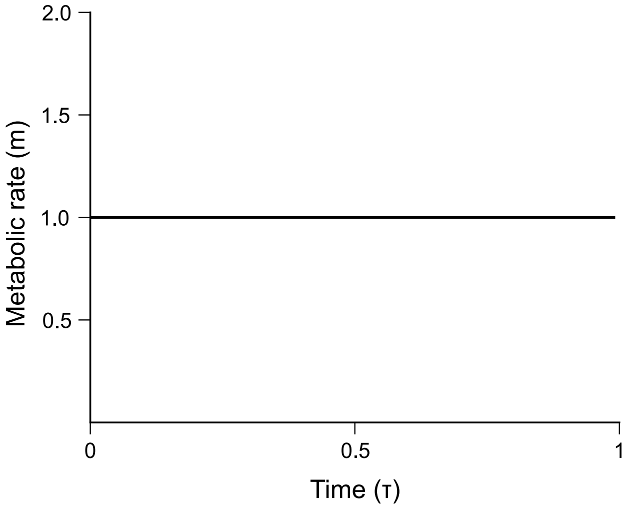


Figure 2: Uniform metabolic rate function; the speed of metabolic activity remains constant during the whole period. (Parameters: g_a=1, g_d=0, H_a=280, H_d=0, α=1/290, β=0)

3.2 Stepwise metabolic rate

Other conditions favour the evolution of a stepwise changing metabilic rate (Figure 3). The speed of metabolic activity does not change within the seasons, but changes abruptly at the end of seasons. The conditions favouring its emergence are:

(a) there is some temperature difference between the two seasons and the cost of metabolic activity is large,

(b) there is some resource renewal rate difference between the seasons and the cost of metabolisms is negligible.

The first condition leads to seasonally changing metabilic rate, because the large cost does not favour any deviances from the periodically changing passive metabolic level. In the second case, the driving force is the periodically changing resource renewal rate instead of a changing passive metabolic activity level; due to the low implied cost individuals optimise their resource consumption by rapidly increasing or reducing their metabolic rate.

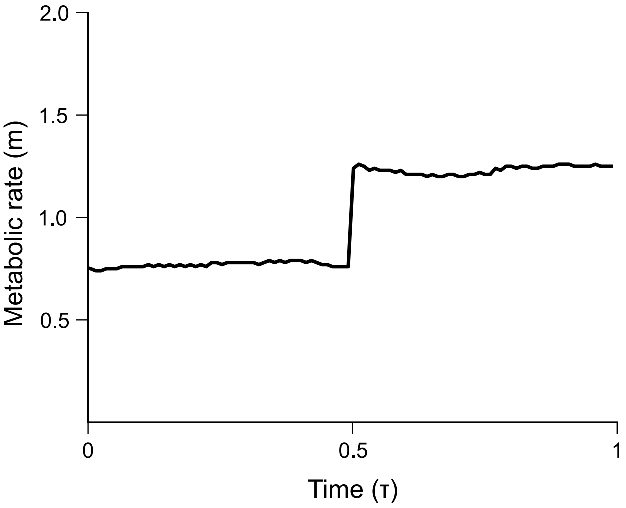


Figure 3: Stepwise metabolic rate function; the speed of metabolic activity changes between the seasons, but remains constant within them. (Parameters: g_a=1, g_d=0.5, H_a=290, H_d=0, α=1/290, β=0)

3.3 Overshooting metabolic rate

Under some special conditons, the evolutionarily stable metabolic function does not only exhibit interseasonal changes, but also changes within the two seasons (Figure 4). At the beginning of a resource abundant season, the metabolic rate sharply increases, which is followed by a slower decreasing. On the contrary, at the beginning of the harsh season, a rapid decreasing is followed by a slower increasing. This kind of metabolic strategy evolves only if there is large resource renewal rate difference between the seasons, and the cost of metabolic activity is moderate.

The interpretation of the evolution of this metabolic function is that in case of favourable environmental changes, it might be beneficial to increase the metabolic rate in order to maximalise the resource uptake. The benefits of increased resource intake can temporally outweigh the moderate cost of increased metabolism. As the population size starts to increase, the benefits gradually decrease until the point when the population can consume all the resources with a metabolic activity level of zero cost. The minimum peak in metabolic rate at the beginning of the harsh seasons can be interpreted in a similar way.

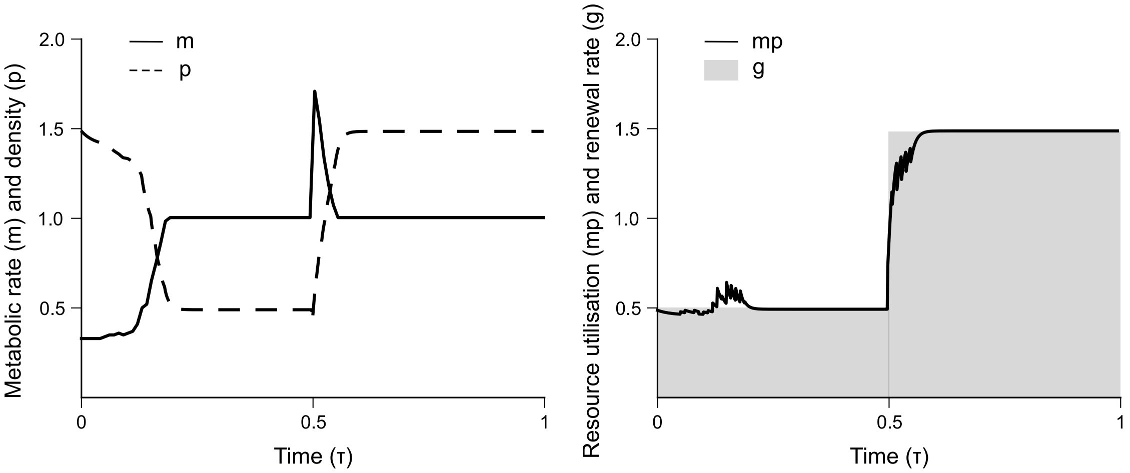


Figure 4: Overshooting metabolic rate function: the speed of metabolic activity exhibits a positive or negative peak at the beginning of seasons, which is followed by a slower relaxation. (Parameters: g_a=1, g_d=1, H_a=290, H_d=0, α=1/290, β=0.1)

This interpretation assumes that the very rapid environmental condition shifts have an important role in the process. In order to investigate it, we compared the evolution of metabolic function in three environments, which differed in how smoothly the environmental conditions change. The reference case was a parameter combination in the above list (Table 1), while in the other two environments the resource renewal rate function was obtained by smoothing the one in the reference case by a boxhat function of smaller and larger width.

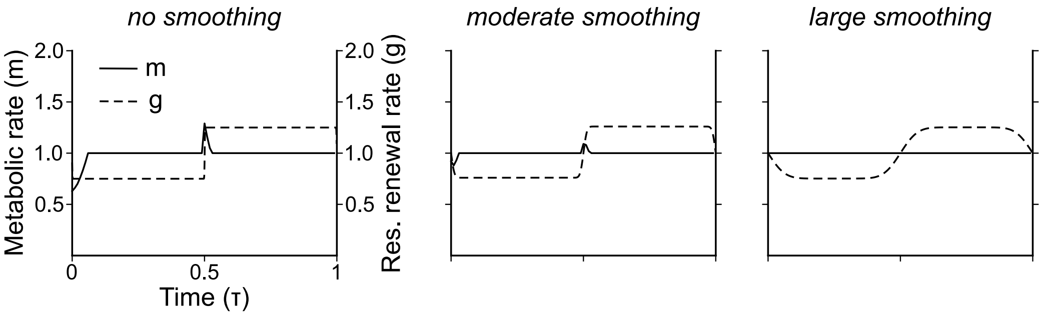


Figure 5: The effect of the resource renewal function smoothing. (Parameters: g_a=1, g_d=0.5, H_a=290, H_d=0, α=1/290, β=0.1, smoothing by boxhat function widths 0, 0.01, 0.05, respectively)

Figure 5 shows that slower environmental changes lead to disappearing positive and negative peaks. It happens because in case of slow environmental changes, population density changes are fast enough compared to the environmental changes so that the population can adapt to the changing resource levels without a need of altered metabolic speed.

4 Discussion

With an evolutionary analysis of a modified MacArthur model, we examined the diversity and main features of the theoretically expected, evolutionarily stable, metabolic rate functions. The parameters of the model were the resource renewal rate, the cost of metabolism and the ambient temperature. Among the many outcomes obtained by using different parameter combinations we could distinguish three main types of optimal metabolic patterns.

The first two types of metabolic functions supported previous results (Szabó, 2015); in favourable and unfavourable environments higher and lower metabolic rate is beneficial, respectively. A homogeneous metabolic function is expected to evolve if either the cost of changing the metabolic rate from the constant passive level is large compared to seasonal resource renewal rate changes or if metabolic costs are negligible while there are no seasonal resource renewal rate changes. The evolution of a seasonally changing metabolic function is favoured in two cases. First, it evolves if the environmental temperature changes, while the implied costs of deviating from the environmentally determined metabolic speed would be too costly. Second, a seasonally actively increased or decreased metabolic rate is favoured if its implied costs are small as compared to resource renewal rate changes. Shortly, the evolution of a heterogeneous metabolic pattern can be triggered by heterogenities in at least one of the environmental functions, ambient temperature and resource renewal rate. Under certain environmental conditions, however, a bit more sophisticated, at first sight counterintuitive metabolic function is favoured. This type exhibits a positive or negative peak when the seasons change. A positive peak occurs, when at the beginning of a good season, it is beneficial to raise the metabolic rate temporally, in spite of its costs, to maximalise resource uptake. Meanwhile the population size increases, so due to the diminishing returns, metabolic rate should be lowered to the passive level determined by ambient temperature to suffer no additional metabolic cost. The sharpness of environmental changes have an important role in this process. We verified that with increasing smoothing of the resource renewal rate function, so making the environmental changes slower, the peak disappears. This supports our theory, that the sudden, sharp change in resource renewal rate is responsible for the emergence of metabolic peaks.

4.1 Interpretation of classic metabolic categories

It is tempting to interpret classic metabolic categories of organisms (ectothermy and endothermy) in light of our results. However, the categories of our model are defined by their metabolic rates, in contrast to the classic metabolic categories defined in terms of body temperature and ambient temperature.

Ectotherms can not use internal energy sources to control their body temperature in a notable extent. The fluctuating environmental temperature affects their body temperature, along with their metabolic rate. In other words, their metabolic rate roughly follows the passive metabolic activity level. In our model, this means a uniform metabolic rate function if the ambient temperature is constant, and a stepwise metabolic rate function if the passive metabolic rate changes seasonally.

Endotherms use internal energy sources to keep their body temperature constant. According to this definition and our interpretation of metabolic activity, endotherms exhibit constant metabolic rate throughout the year. Sensu lato, endothermy means that they can control and set their body at a metabolically favourable temperature by internal bodily processes. If the resource renewal rate is high, it is beneficial to set the metabolic rate high, let alone ambient temperature. Their metabolic pattern can take any form that is evolutionarily beneficial, what makes them fit all our main metabolic rate functions. For example, their metabolic rate can be: uniform, when both environmental functions are constant; stepwise, when resource renewal rate and ambient temperature are seasonally changing; and overshooting, when the resources suddenly arise at the beginning of the favourable season. So endothermy can be interpreted as an evolutionary adaptation enabling a more favourable metabolic function under conditions, when it requires energetic efforts. Heterotherm organisms are also worth mentioning. They can show both traits of an ectotherm and an endotherm. Their metabolic rate changes with the ambient temperature when resting, otherwise they keep their metabolic rate constant.

Note, however, that there are definitely other selective forces behind the evolution of body temperature. Endotherms, sensu stricto maintain constant body temperature, that can be beneficial because, for example, the enzymes can adapt to a specific temperature, without the need to be functional within a broad temperature range.

4.2 Examples

It is hardly imagineable that an absolutely uniform metabolic rate pattern would occur in nature due to the universality of environmental heretogenities. Nevertheless, considering a very homogeneous environment, constant-like metabolic patterns can emerge. It means that there is no need for the organism to change the speed of their metabolic activity throughout the year. Mautz et al. (1992) found a similar metabolic pattern in captive female white-tailed deer *(Odocoileus virginianus)*. They measured metabolic rate by indirect respiration calorimetry, ensuring that seasonal comparisms were made among values within the thermal neutral zone. Due to their methodology, metabolic rate was not influenced by either food or temperature. They found that there were no significant metabolic rate differences between seasons. In other words, the speed of metabolic activity of these captive white-tailed deer did not change significantly through the year.

The second main metabolic function is named stepwise metabolic rate function. Several studies described metabolic patterns of this type. Ruiz et al. (1992) examined the metabolic rate of the flat oyster *(Ostrea edulis)*. This oyster was found to be an opportunist organism which focuses its reproductive efforts during a short resource rich period. Available food was found to be a very important factor for gonad growth, larvae were also released when food density was high. These resource rich seasons were found to be mostly spring and summer. Low resource levels were measured during autumn and winter. In these seasons the flat oyster lived up its energy reserves, which were built up in spring and summer. This is a case when the ruling, most important factor is resource abundance which changes between seasons. Mud crabs *(Scylla paramamosain)* from China (Liu et al., 2013) exhibited a similar metabolic pattern. In this study, metabolic rate was expressed by the speed of mitochondrial processes and metabolic enzyme activity of the animals. It was shown that temperature had the greatest effect on the metabolism and this way also on the farming of these crabs. Simčič and Brancelj (2001) investigated the seasonal changes of the daphnia community in a lake. They measured the oxigen respiration and the respiratory electron transport system (ETS)-activity for a year. They found that the in situ temperature explained a significant part of the variances in the oxigen respirations and the ETS value. As they expected, with higher temperature, these values mostly increased. Thus basically, when the lake's temperature was high and low, the metabolic rate was high and low, respectively.

The third type of metabolic functions exhibited a positive or negative peak at the beginning of seasons. Phytoplankton showed a similar metabolic pattern (Devol, 1979). Their life is dependent on the water's temperature and the amount of nutrients. When the water gets warmer and the nutrient level (mostly limiting nutrient is phosphorus) rapidly increases, these phytoplankton species grow and reproduce with insane intensity which is called blooming. In Findley Lake, lower phosphorus contentration resulted in a smaller peak. After blooming, their respiration decreased, but remained higher than in cold months. However, since net phytoplankton respiration rates were measured, it is hard to determine how much the two factors – population density and metabolic rate – contributed to net respiration. Plus, it is imagineable, that the peak emerged solely because of the changing amount of limiting resources. Another example may be the woodchuck (Bailey, 1965). During an experiment, the researchers did not allow the usually hibernating groundhog to hibernate in the cold seasons. They were kept in a laboratory under constant conditions, regarding temperature, food quantity and food quality. The metabolic rate was observed via CO2 production, which was decreasing from May to February then increasing until May, where it peaked. This pattern resembles of our overshooting type. According to the article, the metabolic changes could be triggered by the changing photoperiod.

5 Conclusions

In our study we presented a model that can describe the evolutionarily stable metabolic patterns in different environments. Among the numerous outcomes, we could separate three main categories. The comparison of the homogeneous and heterogeneous type supports the traditional view; the metabolic rate should be increased or decreased in line with the abundance of resources. However, considering the implied costs, whether this is advantageous or not, also depends on the ambient temperature. Therefore the heterogenity in the speed of metabolism could be triggered by both the seasonality of ambient temperature or the amount of resources. The third category shows that in some cases it is evolutionarily advantageous to have a positive peak of metabolism at the beginning of the favourable season to take advantage on the suddenly increased resources. The negative peak can be interpreted similarly. According to our model, the metabolic function of species can be an important species specific trait, that might be partly responsible for the evolution of endothermy. Note, however, that organisms are diverse and applying the results of our model to particular species needs precautions.

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